THE ARACHNID FOSSIL RECORD

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Arachnids belong to the arthropod phylum Chelicerata which, in addition to the scorpions, spiders, mites and others, embraces the extinct eurypterids, the king-crabs (Xiphosura), and arguably the pycnogonids (sea-spiders). Before presenting a review of the recent discoveries which extend and modify the traditional picture of arachnid evolution, let us first look at the eurypterids and king-crabs.

The eurypterids, or sea-scorpions, are known from rocks ranging from Ordovician to Permian in age (Fig. 1) but are most abundant in upper Silurian strata in Britain, Scandinavia and the USA. Indeed, their distinctive appearance (scorpion-like but with broad swimming paddles in place of the last pair of legs) and abundance in Silurian limestones in the north-east USA has earned one species, *Eurypterus remipes* De Kay the title of State Fossil of New York. This part of the world has also yielded the giant *Buffalopterus* which at 2 m in length was the largest arthropod which ever lived. Its fearsome, huge chelicerae exemplify just one of the methods of prey-capture of these giant carnivores of mid-Palaeozoic seas. Though rare as fossils, eurypterids are usually very well preserved, and one species, *Baltoeurypterus tetragonophthalmus* (Fischer), has provided a wealth of information about the mode of life and palaeoecology of these fascinating animals (Selden, 1981, 1984).

Traditionally allied with the eurypterids in the class Merostomata are the king-crabs, typified by the living *Limulus polyphemus*. The oldest xiphosurans are Cambrian in age, and forms closely similar in morphology and ecology to the living species have been found in rocks as old as Carboniferous, hence *Limulus* is often dubbed a 'living fossil'. The oldest member of the superfamily Limuloidea was described recently from Scotland (Waterston, 1985), and a slightly younger but giant form is now known from Weardale (Siveter & Selden, 1987).

Scorpions have generally been considered the most primitive of arachnids; many authors (e.g. Bristowe, 1958; Grasshoff, 1978) have considered them as the sister-group of the eurypterids, in which case the eurypterids must be included in the Arachnida, or the scorpions excluded from that group. Alternative opinions (Boudreaux, 1979; Weygoldt, 1980; Weygoldt & Paulus, 1979) place the eurypterids as the sister-group of the arachnids (including scorpions); under either scheme, the Merostomata becomes an unnatural group.

Modern scorpions are mainly tropical, nocturnal, terrestrial animals particularly adapted to arid environments and are classified into less than a dozen families. However, fossil scorpions are known from rocks as old as late Silurian; at that time they lived in water alongside their eurypterid relatives, and aquatic scorpions persisted possibly into Mesozoic times. Air-breathing scorpions apparently appeared in the early Carboniferous, and scorpions were at their most diverse in the late Carboniferous when 25 families have been recognized (Kjellesvig-Waering, 1986). Living scorpions can be searched for at night with a blacklight, since they fluoresce in ultraviolet light. This is a property of one layer in their exoskeleton: the hyaline exocuticle. Hyaline exocuticle seems to be unique to scorpions, but is possibly present in eurypterids and king-crabs also. Scraps of scorpion cuticle are abundant in coals and related sediments to the exclusion of all other arthropods, a phenomenon which is attributed to the inertness of the hyaline exocuticle (Bartram *et al.*, 1987) and helps to explain the relative abundance of scorpions amongst arachnid fossils.

Other arachnids have very sporadic fossil records (Fig. 1), though there is a general trend which can be attributed almost entirely to the time distribution of the rare localities in which they are found. Spiders are abundant in some Tertiary (Palaeogene and Neogene) ambers (Oligocene, Baltic and Dominican Republic for example), and are known from shales of the same age in Colorado. Tertiary faunas

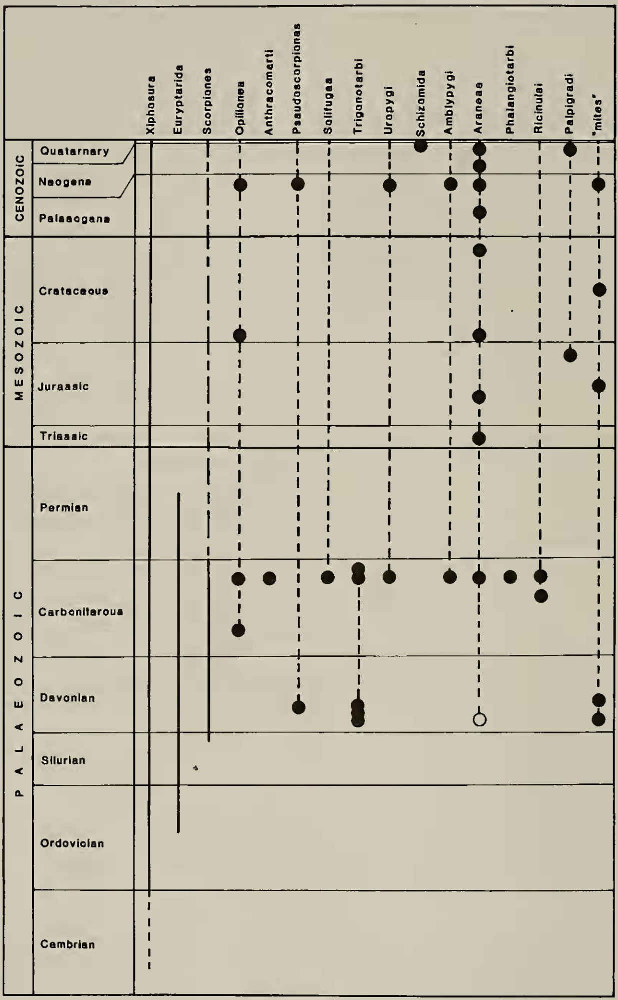

Fig. 1. Known stratigraphic ranges of the major groups of chelicerates, from published and unpublished data. Solid lines indicate fairly continuous occurrence, dashed lines indicate data poor or lacking. Solid circles mark only or most important occurrences, open circle indicates uncertain occurrence.

are more similar to those of today than to Mesozoic and Palaeozoic faunas. The end-Cretaceous mass extinction brought the Mesozoic era to a close and the faunal and floral changes across this boundary are great. Unfortunately, Mesozoic arachnids are exceptionally rare, so we cannot be sure whether the same is true of them. Incidentally, Cretaceous ambers are known from Canada and the Lebanon which contain spider inclusions, so it may not be very long before we have enough well preserved specimens to test this hypothesis.

In the last few years, four spider specimens from early Cretaceous lithographic limestone of the Sierra de Montsech in north-east Spain have been discovered. This locality has long been famous for its beautifully preserved plants, insects, amphibians, and especially bird feathers. Three of the spiders are mature males with their distinctively elaborate palps, and the fourth has characters which could place it in a modern family. A major problem with these Mesozoic spiders is that the details needed to place them in the classification scheme for Recent spiders are not always preserved. In a Jurassic example (Eskov, 1984), a combination of characters of numerous living families was observed which resulted in the setting up of a new 'extinct' family.

Travelling further back in time we pass the end-Permian extinction event, the most severe of all, and come to the late Carboniferous. Ironstone nodules in coal measure rocks of Europe and North America have yielded an abundant terrestrial and near-shore fauna, including crustaceans, insects, millipedes, xiphosurans and arachnids. Particularly interesting are the 20 or so specimens of ricinuleids. Ricinuleids are charming little thick-skinned arachnids which creep amongst leaf litter under logs and in caves in the American and West African tropics. There are about 50 living species in three genera. The Carboniferous ricinuleids are remarkably similar to the living forms; an interesting difference being that the fossils show two pairs of eyes in the position on the living animals where vestigial eye-spots are present (Selden, 1986).

Another group of arachnids relatively well-represented in Coal Measure rocks are the extinct trigonotarbids. These animals are very close to spiders in their morphology, but lack spinning organs. Trigonotarbids are also a major component of the terrestrial faunas of three important Devonian localities: the Rhynie chert of Aberdeenshire; Alken-an-der-Mosel, Germany; and Gilboa, New York. Hirst (1922) described the Rhynie fauna, a bog habitat of early vascular plants rapidly engulfed in hot, siliceous waters from nearby volcanic eruptions. The Rhynie chert contains the oldest terrestrial fauna known, and includes a springtail, a mite, numerous trigonotarbids, and a possible spider (see Rolfe, 1980 for review of this and other early terrestrial faunas). The Alken fauna includes both terrestrial (trigonotarbid, myriapod) and amphibious (eurypterid) elements (Størmer, 1970–6).

More recently, palaeobotanists Bonamo and Grierson were dissolving grey siltstones from the Devonian of Gilboa, New York for early vascular plants when they came across an extremely varied fauna of early land animals (Shear *et al.*, 1984; Shear, 1986). Again, trigonotarbids are very common (Shear & Selden, 1986), but there is also evidence of insects, myriapods (the earliest centipede), scorpions, and mites. The fossils are beautifully preserved, and when mounted in balsam and viewed in transmitted light, minute details of setae, trichobothria, slit sensillae, lyriform and other sense organs are clearly visible (see Shear *et al.*, 1988).

One element of the fauna caused the greatest modification to the arachnid fossil record when first discovered. Two beautiful little creatures, described by the assistant who found them as 'little dragons', turned out to be pseudoscorpions.

Virtually identical in all aspects to living pseudoscorpions, the find of these Devonian forms pushes the fossil record of the group back tenfold.

Exciting though these finds of rare, earliest terrestrial arachnids are, their importance to Zoology extends beyond that to Arachnology alone. They help us to understand how the very first land animals pioneered the empty terrestrial habitat 400 million years ago. It was these pioneers which paved the way for the rich and varied arthropod fauna which abounds in our countryside today.

References

Bartram, K.M., Jeram, A.J. & Selden, P.A. 1987. Arthropod cuticles in coal. *J. Geol. Soc. London* **144**: 513–517.

Boudreaux, H.B. 1979. Significance of intersegmental tendon system in arthropod phylogeny and a monophyletic classification of Arthropoda. In Gupta, A.P. (ed) *Arthropod Phylogeny*, 551–586. Van Nostrand Reinhold, New York.

Bristowe, W.S. 1958. *The World of Spiders*. Collins, London.

Eskov, K. 1984. A new fossil spider family from the Jurassic of Transbaikalia (Araneae: Chelicerata). *N. J. Geol. Paläont Mh.* **11**: 645–653.

Grasshoff, M. 1978. A model of the evolution of the main chelicerate groups. *Symp. Zool. Soc. Lond.* **42**: 273–284.

Hirst, S. 1922. On some arachnid remains from the Old Red Sandstone (Rhynie Chert Bed, Aberdeenshire). *Ann. Mag. Nat. Hist.* **12**, 455–474.

Kjellesvig-Waering, E.N. 1986. A restudy of the fossil Scorpionida of the world. *Palaeontographica Americana* **55**: 1–287.

Rolfe, W.D.I. 1980. Early invertebrate terrestrial faunas. In: Panchen, A.L. (ed.) The terrestrial environment and the origin of land vertebrates. *Syst. Assoc. Spec. Vol. No. 15*, 117–157, Academic Press, London and New York.

Selden, P.A. 1981. Functional morphology of the prosoma of *Baltoeurypterus tetragonophthalmus* (Fischer) (Chelicerata: Eurypterida). *Trans. R. Soc. Edinb., Earth Sciences* **72**: 9–48.

Selden, P.A. 1984. Autecology of Silurian eurypterids. *Spec. Paps. Palaeont.* **32**: 39–54.

Selden, P.A. 1986. Ricinuleids — living fossils? *Actas X Congr. Int. Aracnol., Jaca, España* **1**: 425.

Shear, W.A. 1986. A fossil fauna of early terrestrial arthropods from the Givetian (upper Middle Devonian) of Gilboa, New York, U.S.A. *Actas X Congr. Int. Aracnol., Jaca, España* **1**: 387–392.

Shear, W.A., Bonamo, P.M., Grierson, J.D., Rolfe, W.D.I., Smith, E.L. & Norton, R.A. 1984. Early land animals in North America: evidence from Devonian age arthropods from Gilboa, New York. *Science* **224**: 492–494.

Shear, W.A. & Selden, P.A. 1986. Phylogenetic relationships of the Trigonotarbida, an extinct order of arachnids. *Actas X Congr. Int. Aracnol., Jaca, España* **1**: 393–397.

Shear, W.A., Selden, P.A., Rolfe, W.D.I., Bonamo, P.M. & Grierson, J.D. 1987. New terrestrial arachnids from the Devonian of Gilboa (Arachnida, Trigonotarbida). New York. *Novitates* **2901**: 1–74.

Siveter, D.J. & Selden, P.A. 1987. A new, giant, xiphosuran from the lower Namurian of Weardale, County Durham. *Proc. Yorks. geol. Soc.* **46**: 153–168.

Størmer, L. 1970, 1972, 1973, 1974, 1976. Arthropods from the Lower Devonian (Lower Emsian) of Alken-an-der-Mosel, Germany. Parts 1–5. *Senckenberg. leth.* **51**: 335–369; **53**: 1–29; **54**: 119–205, 359–451; **57**: 87–183.

Waterston, C.D. 1985. Chelicerata from the Dinantian of Foulden, Berwickshire, Scotland. *Trans. R. Soc. Edinb., Earth Sciences* **76**: 25–53.

Weygoldt, P. 1980. Towards a cladistic classification of the Chelicerata. *8th Int. Congr. Arachnol., Vienna*, 1980, 331–334.

Weygoldt, P. & Paulus, H.F. 1979. Untersuchungen zur Morphologie, Taxonomie und Phylogenie der Chelicerata. *Z. Zool. Syst. Evolut.-forsch.* **17**: 177–200.